

Article



Assessment of Tomato Recombinant Lines in Conventional and Organic Farming Systems for Productivity and Fruit Quality Traits

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Abstract: It is estimated that more than 95% of organic agriculture is based on crop cultivars that were bred for the conventional high-input sector. Most selections were made through conventional breeding programs and lack important traits required under organic and low-input conditions. Hybrids are the most common type of cultivars used in tomato because of heterosis. In tomato, continuous selfing enabled homozygosity to exploit favorable additive genes, resulting in the so-called inbred vigor. This paper presented the possibility to express inbred vigor at a level equal to or greater than hybrid vigor in tomato when cultivated under organic low input conditions. The evaluation of the recombinant lines produced through classical reverse breeding from four F₁ single cross hybrids was done at low- and high-input farming systems. The results show that, following the appropriate breeding process in early generation selection and under low-input conditions, it is possible to produce recombinant lines, demonstrating inbred vigor in yield potential and fruit quality. These genetic materials can stand as new dynamic cultivars intended for cultivation in organic, low-input, or high-input conditions, depending on their performance in different farming systems at the later stages of evaluation.

Keywords: inbred vigor; heterosis; hybrid vigor; tomato; recombinant lines; low inputs; organic culture

1. Introduction

There is a broad consensus on the significance of sustainable farming in economic planning and human development [1,2]. A significant cause of failure to arouse enthusiasm is the lack of available cultivars for the particular requirements of sustainable agricultural systems [3]. Nowadays, there are not many cultivars specifically bred for organic and low-input systems in developed countries [4]. It is estimated that more than 95% of organic agriculture is based on crop cultivars that were bred for the conventional high-input sector with selection in conventional breeding programs and lack important traits required under organic and low-input production conditions [5,6].

Depending on the crop, the cultivars grown are either mono-genotypic like inbred pure lines, single-cross hybrids, and clones, or poly-genotypic, such as open-pollinated populations, multi-line mixtures, and synthetic cultivars [7,8]. Cultivated tomato (*Solanum lycopersicum* L.) is grown as inbred pure lines or singe-cross hybrids and it is one of the most important and popular vegetable crops grown under low- and high-input environments worldwide because of its high nutritional value [9–11]. In tomato, commercial seed companies commonly rely on hand labor to produce the F₁ hybrid seed. Most current commercial tomato cultivars are hybrids, but many organic growers in the U.S.A. and some small growers in Europe want to save and keep their own seed (pure lines cultivars).



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Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/). Generally, there will be a need for both types of cultivars, depending on growers' needs and market and consumer demands [4].

Hybrids are the most common type of cultivars used in tomato because of heterosis. Heterosis in plants is a well-studied phenomenon expressed in hybrids, which are more productive than their parents [12]. Hedrick and Booth [13] were the first to observe hybrid vigor in tomato, and many investigators further confirmed this phenomenon [14,15]. Hybridization proved a crucial tool, facilitating a yield increase from 30% to 400%, enriching many other desirable quantitative and qualitative traits in crops [11]. However, hybrid seed production is a sophisticated technology and a cost-intensive venture. Only well-organized seed companies can afford hybrid seed production with adequate scientific personnel and well-equipped research facilities.

Fasoulas [16], in his effort to explain the superior performance of hybrids, proposed a pyramidal evolution pattern categorizing crops into four main groups [17]. The higher the position of a crop in the pyramid, the higher its position in the evolutionary scale, and the smaller the load of deleterious genes it carries. Inbred line cultivars in autogamous crops, such as tomato, belong to the extreme of the mono-genotypic cultivars [7] carrying the lowest load of deleterious genes. In this group, continuous selfing, applied after natural or artificial selection, enabled homozygosity to exploit favorable additive genes. The predominance of inbred lines in this group is attributed to the increased amount of the gene product owing to their additive homoallelic complementation, resulting in the so-called inbred vigor [17]. This becomes feasible by the systematic removal of deleterious genes and their replacement by favorable additive alleles [17].

Tomato is tolerant to inbreeding, and this allows the generation and maintenance of inbred lines. Therefore, genetic variability recombination represents an excellent alternative for obtaining superior genotypes [18–20]. Tomato inbred-recombinant lines have many advantages that are important for developing sustainable agriculture: (1) they breed true to type and have a low cost of certified seed production, and (2) producers may retain their own seed for the next season. This is extremely important for poor small-scale farmers in developing countries. Moreover, the homozygotic structure of inbred line cultivars enables them (3) to display high and stable yield and (4) to exhibit high tolerance or resistance to biotic and abiotic stresses if they carry favorable additive genes [7].

This work aims to evaluate the possibility of maintaining or increasing inbred vigor to reach the yield potential of F_1 hybrids and produce inbred tomato lines with the dynamic of hybrids in productivity and fruit quality characteristics. Following different breeding approaches, different types of recombinant (Half-sib, isogenic) lines were produced and evaluated under two different farming systems. The design of experiments helps to find the most suitable type of tomato cultivar per each farming system according to the high (conventional) or low (organic) level of inputs used by farmers.

2. Materials and Methods

2.1. Plant Material

The commercial F_1 single-cross hybrids 'Iron', 'Sahara', 'Formula', and 'Elpida' were used as the main source of genetic material. The above cultivars occupy 20% (cvrs. 'Iron' and 'Sahara') and 50% (cvrs. 'Formula' and 'Elpida') of the total tomato cropping area in Greece [21]. The traditional cultivar 'Makedonia', one of the best tomato inbred lines in Greece, was used as control. 'Makedonia' is a cultivar developed by selection using the pure line breeding method in a local tomato population at the Agricultural Research Center of Northern Greece (ARCNG). This interesting tomato cultivar was widely used in the traditional farming and low-input cropping systems of the previous era, before high-input agricultural systems were most commonly used. 'Makedonia' is indeterminate and welladapted to both glass-covered and open-field cropping conditions of the Mediterranean region. It is characterized by preferable physicochemical and sensory properties with attractive and tasty fresh fruits.

2.2. Methodology

Regarding the first two hybrids ('Iron', 'Sahara'), mass selection was applied for two generations to produce F_3 segregating generation, and this was followed by recurrent selection to produce HS_5 recombinant lines. These recombinant lines were produced after pollination of selected plants by a mixture of pollen from the previous cycle's selected plants. Pollen donors were those plants that had the desired performance in terms of yield components and fruit quality characteristics [22]. Finally, two recombinant half sib tomato lines from each of the two parental hybrids were selected.

In order to select another two commercial tomato hybrids that resemble the previous ones in the size of the inbreeding depression that occurs in the F_2 generation, an experiment was performed to evaluate 20 commercial tomato hybrids. The results of this evaluation indicated the selection of F_1 'Formula' and F_1 'Elpida' hybrids for continuing the breeding process. Pedigree selection was applied for two seasons for these two hybrids under low plant density in a honeycomb design, and this was followed by pedigree selection and evaluation of progenies under high-density conditions using randomized complete block design (RCBD) (Figure 1). At the end of all pedigree processes (F_5), eight recombinant lines from each hybrid were selected based on all the desirable characteristics, including earliness, productivity, and fruit quality traits.

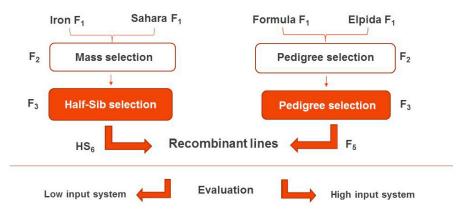


Figure 1. Breeding process applied for the production of new recombinant lines.

2.3. Selection and Assessment Procedure

Two experiments were established under different farming systems (i.e., conventional high-input and low organic input) to study the selected recombinant lines' performance. Those lines were obtained from the commercial single-cross hybrids ('Iron', 'Sahara', 'Formula', and 'Elpida'), as mentioned previously.

2.3.1. Farming System 1: Conventional with High-Input Conditions

The conventional experiment was conducted in a heated greenhouse on a private farm in Preveza, West Greece. The experimental plant material was prepared conventionally. Uniform seedlings were hand transplanted on 15 April 2015, at an intra-row distance of 0.5 m and an inter-row distance of 1 m (2 plants/m²). The high wire one-stem training system was applied. The greenhouse was shaded in June, July, and August. An RCBD was used, with three replications, each consisting of ten plants. Practices following the high-input cultural system include the use of synthetic fertilizers and use of chemical pesticides according to a weekly conventional program. The total amount of N, P₂O₅, and K₂O applied to the conventional system in each growing season was 130, 150, and 150 kg ha⁻¹. All the observations and measurements were obtained on an individual plant basis. Yield components, earliness, and fruit quality traits of table-ripe fruit were recorded for each entry.

2.3.2. Farming System 2: Organic (Low-Input Cultural Practices)

The low-input experiment was conducted in a non-heated greenhouse at the Agricultural Research Center of Northern Greece (ARCNG), in Thermi-Thessaloniki, following a similar experimental design as described previously. Organic (low-input) cropping practices were followed for irrigation, fertilizer, and pesticide application. The cropping practices applied were identical to organic farming principles (field rotation with legumes, manure, soil mulching using a biodegradable film, and no chemical or agrochemical applications). Composted poultry manure was applied at 3 t ha⁻¹ (dry weight). All the observations and measurements were obtained on an individual plant basis. For each entry, yield components, earliness, and fruit quality characteristics of table-ripe fruit were evaluated.

2.4. Traits Evaluated

Table-ripe fruit yield was measured on a per plant basis over six harvest dates in all experiments. Earliness and total yield were estimated based on production (g), which was based on harvests until 75 and up to 100 days after transplanting, respectively. All table-ripe fruits harvested were transferred to the laboratory of ARCNG, where they were counted, graded into different classes according to quality standards and sensitivity to physiological disorders, and weighed. The total solids (TS) were determined on blended samples of each fruit after oven drying at 70 °C. The total soluble solids (TSS) were determined using an Atago PR-100 hand refractometer on the juice taken from the above samples.

2.5. Statistical Analyses

Data were subjected to analysis of variance procedures (ANOVA) and Scott–Knott cluster test at 5% probability and significance level. For determination of the stability of performance, the variables total and early yield were used. The stability of performance was defined by the standardized mean (i.e., $\bar{\mathbf{x}}/\mathbf{s} = \text{mean/standard}$ deviation) of individual plants [23], which is the reciprocal of the coefficient of variability (CV) among individual plants of a crop stand. In the case of cultivars, the one combining the largest mean yield $\bar{\mathbf{x}}$ with the largest $\bar{\mathbf{x}}/\mathbf{s}$ is the most productive and stable across environments [23]. This ratio, $\bar{\mathbf{x}}/\mathbf{s}$, is also a way of estimating the genetic yield improvement [24]. The correlations between the characteristics were made using the Pearson correlation coefficient (rp) [25] and were determined for significance level a = 0.05 (*) or a = 0.01 (**). For the simultaneous evaluation of yield and stability across environments, a genotype and genotype × environment (GGE) biplot analysis [26,27] was conducted using Genstat (13).

3. Results

3.1. Farming System 1: Conventional High-Input System

In the high-input cropping system, all recombinant lines originating from 'Formula' hybrid lagged significantly from the F_1 hybrid for early yield, with an average inbreeding depression of 57%. This lag is probably due to the simultaneous effect of the main yield components, with average inbreeding depression in the number of fruits per plant (44%) and total fruit weight (23%) (Table 1).

In comparison, the recombinant lines originating from 'Elpida' hybrid had a similar or significantly better behavior than the parental F_1 hybrid. In fact, lines 3 and 7 exhibited an inbred vigor of 9% and 20%, mainly due to a significant vigor increase of 21% and 30% in the number of fruits per plant (Table 1).

Entry	Early Fruit Yield in High Inputs									
	g/Plant			Fruit Number/Plant			g/Fruit			
	x	V/D	⊼/s	$\overline{\mathbf{x}}$	V/D	⊼/s	x	V/D	⊼/s	
Formula F ₁	2540.13 a *	100	3.01	11.40 a	100	3.35	220.67 a	100	6.3	
Formula F ₅ -1	1111.60 c	44	2.78	7.20 b	63	3.53	156.67 b	71	3.2	
Formula F ₅ -2	1025.60 c	40	2.29	6.80 b	60	2.16	163.20 b	74	2.6	
Formula F ₅ -3	512.70 c	20	2.14	3.57 b	31	2.59	145.03 b	66	2.6	
Formula F ₅ -4	1087.87 c	43	1.70	5.33 b	47	1.98	196.20 a	89	6.4	
Formula F ₅ -5	861.07 c	34	1.72	4.80 b	42	1.96	177.20 b	80	3.6	
Formula F ₅ -6	1207.43 c	48	2.56	7.93 b	70	3.58	150.60 b	68	4.8	
Formula F ₅ -7	858.53 c	34	1.74	5.20 b	46	2.40	167.37 b	76	2.9	
Formula F ₅ -8	1956.6 b	77	3.36	10.50 a	92	2.47	198.90 a	90	4.5	
Elpida F ₁	2018.37 b	100	2.69	9.33 a	100	3.28	212.60 a	100	6.8	
Elpida F ₅ -1	1600.13 b	79	3.51	10.13 a	109	3.56	163.80 b	77	3.5	
Elpida F ₅ -2	1644.73 b	81	2.47	10.93 a	117	2.92	152.03 b	72	3.7	
Elpida F ₅ -3	2194.60 a	109	2.39	11.33 a	121	2.34	194.47 a	91	5.2	
Elpida F ₅ -4	1479.27 b	73	2.81	8.93 a	96	2.96	172.70 b	81	3.4	
Elpida F ₅ -5	886.10 c	44	2.45	7.77 b	83	2.21	127.33 b	60	2.6	
Elpida F ₅ -6	1725.27 b	85	2.65	12.00 a	129	2.58	149.37 b	70	4.6	
Elpida F ₅ -7	2425.40 a	120	2.73	12.13 a	130	2.88	201.93 a	95	5.4	
Elpida F ₅ -8	1746.60 b	87	1.85	7.47 b	80	1.84	234.73 a	110	4.7	
Iron F ₁	1406.41 c	100	1.77	6.13 b	100	1.92	216.00 a	100	4.9	
Iron HS ₆ -2	811.17 c	62	1.72	5.13 b	84	1.90	152.03 b	70	3.3	
Iron HS ₆ -3	915.37 c	70	2.22	6.27 b	102	2.88	143.23 b	66	4.4	
Sahara F ₁	928.97 c	100	1.71	4.77 b	100	1.62	192.23 a	100	3.4	
Sahara HS ₆ -1	865.77 c	93	1.67	7.67 b	161	1.50	115.17 b	60	3.3	
Sahara HS ₆ -2	901.37 c	97	1.69	5.77 b	121	1.54	165.57 b	86	3.3	
Makedonia	968.80 c	_	1.56	5.60 b		1.97	168.27 b		4.0	

Table 1. Early fruit yield (g/plant, fruit number/plant, and g/fruit), vigor/depression (% of its corresponding hybrid), and stability of performance (\bar{x} /s) of the hybrids and recombinant inbred lines, in a high-input farming system.

* Entries with the same letter within a column indicate not significant differences, according to Scott–Knott cluster test (a = 0.05).

The recombinant lines originating from 'Iron' hybrid did not lag significantly from the F_1 hybrid (30% and 38%). Both recombinant lines originating from 'Sahara' reached the hybrid's early yield performance (3–7% inbreeding depression). The recombinant lines characterized by great earliness were also very stable, reaching the hybrid's stability of performance. Furthermore, most of the recombinant lines exceeded in early yield performance of the control inbred 'Makedonia' (Table 1).

Comparing the response of genetic material used in the high-input system and in terms of total yield, the recombinant lines of 'Formula' F_1 hybrid indicated the most significant inbreeding depression. This situation was mainly owing to the analogous depression in the fruit weight. However, based on the number of fruits per plant, some lines performed better, up to a 19% increase, than the respective hybrid (Table 2).

Four recombinant lines originating from 'Elpida' hybrid were almost better than or equal to the hybrid (Table 2), with three showing an inbred vigor of 1–8%. All lines surpassed the hybrid for the number of fruits per plant (average inbred vigor of 12%). Simultaneously, all the recombinant lines, except line 8, had less fruit weight than the hybrid (Table 2).

	Total Yield in High Inputs									
Entry	g/Plant			Fruit Number/Plant			g/Fruit			
	x	V/D	⊼/s	x	V/D	⊼/s	x	V/D	⊼/s	
Formula F ₁	5542.20 b *	100	7.40	25.17 b	100	6.88	221.53 a	100	10.6	
Formula F ₅ -1	4076.07 c	74	4.37	26.47 b	105	6.02	155.83 с	70	4.41	
Formula F ₅ -2	4075.20 c	74	5.20	27.13 b	108	4.99	152.47 с	69	5.61	
Formula F ₅ -3	2953.97 d	53	2.77	18.43 c	73	2.99	160.13 c	72	4.63	
Formula F ₅ -4	4580.67 c	83	7.12	23.33 b	93	5.77	198.50 a	90	10.0	
Formula F ₅ -5	3860.20 c	70	4.70	24.47 b	97	5.04	158.27 с	71	11.4	
Formula F ₅ -6	4572.73 с	83	7.06	30.03 b	119	5.19	155.10 c	70	8.17	
Formula F ₅ -7	3978.80 c	72	5.33	23.03 b	91	5.78	173.37 b	78	9.67	
Formula F ₅ -8	4052.77 c	73	5.61	22.43 b	89	3.86	185.87 b	84	6.63	
Elpida F ₁	6201.20 a	100	9.88	32.50 a	100	7.64	193.17 a	100	9.7	
Elpida F ₅ -1	5653.87 b	91	5.90	38.47 a	118	6.61	147.97 с	77	7.5	
Elpida F ₅ -2	5127.70 b	83	5.42	36.13 a	111	4.76	145.27 с	75	6.2	
Elpida F ₅ -3	6686.87 a	108	7.34	37.47 a	115	5.66	181.87 b	94	6.2	
Elpida F ₅ -4	6139.07 a	99	5.63	37.60 a	116	7.89	163.07 c	84	8.3	
Elpida F ₅ -5	5242.87 b	85	4.43	38.73 a	119	4.44	136.47 с	71	8.08	
Elpida F ₅ -6	5098.20 b	82	4.98	34.20 a	105	8.11	149.23 c	77	5.9	
Elpida F ₅ -7	6275.73 a	101	6.65	34.20 a	105	8.61	183.53 b	95	10.6	
Elpida F ₅ -8	6685.53 a	108	6.69	34.60 a	106	6.80	195.37 a	101	6.74	
Iron F ₁	5013.07 b	100	5.69	25.33 b	100	4.70	197.77 a	100	7.6	
Iron HS_6-2	3859.57 c	77	4.38	24.13 b	95	4.68	160.13 c	81	9.0	
Iron HS ₆ -3	3678.63 c	73	6.16	24.70 b	98	6.52	150.17 c	76	6.5	
Sahara F ₁	4579.63 c	100	3.52	25.67 b	100	4.54	178.00 b	100	4.0	
Sahara HS ₆ -1	3859.63 c	84	3.46	28.80 b	112	5.79	133.03 c	75	4.5	
Sahara HS ₆ -2	4174.47 c	91	2.90	28.00 b	109	2.61	156.33 c	88	3.5	
Makedonia	2683.27 d	_	2.73	17.70 c		4.01	147.83 c		5.8	

Table 2. Total fruit yield (g/plant, fruit number/plant, and g/fruit), vigor/depression (% of its corresponding hybrid), and stability of performance (\bar{x} /s) of the hybrids and new recombinant inbred lines in the high-input farming system.

* Entries with the same letter within a column indicate not significant differences, according to Scott-Knott cluster test (a = 0.05).

The recombinant lines of 'Iron' lagged significantly behind their parental hybrid, in both total yield (23–27%) and fruit weight (19–24%). Moreover, there was a small, but not significant lag in the number of fruits per plant (2–5%) (Table 2).

Although the recombinant lines of 'Sahara' had slightly less total yield (9–16%), fruit weight and fruits per plant exceeded the parental hybrid by 12–25% and 9–12%, respectively (Table 2).

The new recombinant lines exceeded the total yield of the inbred cultivar 'Makedonia'. Highly stable performance in all three yield components was noticed in all recombinant lines. Almost all recombinant lines had very high stability of performance in all three yield characteristics.

3.2. Farming System 2: Low-Input System

In the low-input cropping system, the recombinant lines derived from 'Formula' showed an inbreeding early yield depression ranging from 1 to 51%, having an average of depression 32% (Table 3). The recombinant lines 4, 6, and 8 did not differ in earliness from the original F₁ hybrid, with recombinant line 8 reaching similar yields as the hybrid grown in this low-input farming system (Table 1). Recombinant line 8 exceeded the hybrid in the number of fruits per plant by 18%, even though it was 16% less productive in fruit weight.

	Early Fruit Yield in Low Inputs									
Entry	g/Plant			FRUI	T Number	/Plant	g/Fruit			
	x	V/D	⊼/s	x	V/D	⊼/s	x	V/D	⊼/s	
Formula F ₁	1393.76 a *	100	3.41	8.24 a	100	3.41	169.70 a	100	5.52	
Formula F ₅ -1	806.63 b	58	2.12	5.38 b	65	2.84	146.63 b	86	4.07	
Formula F ₅ -2	703.07 b	50	2.25	5.07 b	62	2.13	143.54 b	85	4.01	
Formula F ₅ -3	875.00 b	63	3.44	5.20 b	63	4.11	169.46 a	100	5.34	
Formula F ₅ -4	1087.81 a	78	1.95	6.81 b	83	1.99	156.19 a	92	4.81	
Formula F ₅ -5	766.64 b	55	1.17	5.07 b	62	1.19	152.60 b	90	5.11	
Formula F ₅ -6	1254.31 a	90	2.39	9.19 a	112	2.98	135.44 b	80	5.23	
Formula F ₅ -7	686.50 b	49	1.23	5.14 b	62	1.47	122.59 b	72	3.14	
Formula F ₅ -8	1377.56 a	99	2.88	9.69 a	118	2.95	142.63 b	84	5.71	
Elpida F ₁	1079.18 a	100	3.64	7.88 a	100	3.72	137.73 b	100	6.35	
Elpida F ₅ -1	897.47 b	83	2.62	5.82 b	74	2.53	157.80 a	115	5.68	
Elpida F ₅ -2	992.29 b	92	2.35	6.82 b	87	2.29	147.13 b	107	5.81	
Elpida F ₅ -3	1043.31 a	97	2.56	6.94 b	88	2.73	154.17 a	112	4.26	
Elpida F ₅ -4	1114.65 a	103	2.95	6.59 b	84	2.84	177.64 a	129	3.58	
Elpida F ₅ -5	949.00 b	88	1.85	5.75 b	73	2.13	165.66 a	120	3.30	
Elpida F ₅ -6	1308.94 a	121	2.63	7.63 a	97	2.59	173.96 a	126	8.04	
Elpida F ₅ -7	901.47 b	84	1.77	6.60 b	84	2.09	138.57 b	101	2.94	
Elpida F ₅ -8	1023.58 a	95	1.83	6.08 b	77	1.74	174.97 a	127	3.80	
Iron F ₁	771.33 b	100	1.68	5.33 b	100	1.70	149.90 b	100	3.97	
Iron HS_6-2	879.39 b	114	3.34	6.61 b	124	4.95	133.47 b	89	4.48	
Iron HS_6-3	967.53 b	125	2.72	6.76 b	127	3.86	141.54 b	94	4.55	
Sahara F ₁	1511.70 a	100	2.76	9.22 a	100	2.62	164.12 a	100	6.54	
Sahara HS_6^-1	735.81 b	49	1.82	6.25 b	68	1.62	125.34 b	76	3.78	
Sahara HS ₆ -2	1368.43 a	91	3.23	9.93 a	107	2.79	140.72 b	86	7.03	
Makedonia	915.61 b	_	2.11	5.72 b	—	2.36	160.14 b		4.04	

Table 3. Early fruit yield (g/plant, fruit number/plant, and g/fruit), vigor/depression (% of its corresponding hybrid), and stability of performance ($\bar{\mathbf{x}}$ /s) of the hybrids and new recombinant inbred lines, in the low-input farming system.

* Entries with the same letter within a column indicate not significant differences, according to Scott–Knott cluster test (a = 0.05).

The recombinant lines originating from 'Elpida' hybrid had an average early yield reduction of 5% compared with the original F_1 hybrid. Additionally, four recombinant lines did not differ from the hybrid, and two exhibited an inbred vigor of 3–21% (Table 3). This inbred vigor is attributed to the superiority of the aforementioned lines over the hybrid in fruit weight (17% mean vigor). However, there was a reduction in the number of fruits per plant (17% average lag-depression) (Table 3).

The two half-sib lines obtained from 'Iron' exceeded the F_1 hybrid in early yield by 14% and 25%, respectively (Table 3). This superiority is probably due to the high number of fruits per plant, which was observed in these lines compared with the original hybrid (24–27%). In comparison, the two recombinant lines produced from 'Sahara' hybrid both lagged from the original hybrid (9 and 51%, respectively) (Table 3).

Overall, 11 of the 20 recombinant lines selected had greater early yield than the inbred line 'Macedonia'. All recombinant lines had a relatively high stable yield performance (Table 3).

In the low-input cropping system, most of the recombinant lines did not differ from the F_1 'Formula' hybrid for total yield. The recombinant lines had an average lag of only 7% and line 8 exhibited an inbred vigor for total yield of 3%. The aforementioned lines' excellent performance is due to their superiority in the number of fruits per plant, which was improved by 21% compared with the hybrid (Table 4).

Entry	Total Yield in Low Inputs									
	g/Plant			Frui	Fruit Number/Plant			g/Fruit		
	x	V/D	⊼/s	x	V/D	⊼/s	x	V/D	⊼/s	
Formula F ₁	3432.35 a *	100	3.58	18.00 b	100	4.12	190.02 a	100	5.59	
Formula F ₅ -1	3394.56 a	99	4.58	20.00 b	111	4.68	171.95 a	90	5.39	
Formula F ₅ -2	3395.53 a	99	4.39	20.07 b	111	5.46	171.52 a	90	4.68	
Formula F ₅ -3	3240.13 a	94	5.18	17.93 b	100	4.20	185.11 a	97	5.4	
Formula F ₅ -4	3207.50 a	93	3.96	19.50 b	108	3.65	168.78 a	89	5.0	
Formula F ₅ -5	2851.93 b	83	2.24	17.07 b	95	2.64	164.03 a	86	4.7	
Formula F ₅ -6	3311.13 a	96	3.26	21.56 a	120	4.48	152.63 a	80	5.4	
Formula F_5 -7	2689.64 b	78	2.33	17.93 b	100	2.98	147.58 a	78	4.3	
Formula F ₅ -8	3538.75 a	103	5.87	21.81 a	121	4.38	167.15 a	88	4.9	
Elpida F ₁	3717.76 a	100	5.14	23.94 a	100	5.19	156.95 a	100	6.5	
Elpida F ₅ -1	3821.18 a	103	4.58	24.76 a	103	5.35	155.65 a	99	6.3	
Elpida F ₅ -2	3483.47 a	94	4.94	22.18 a	93	4.07	159.84 a	102	7.5	
Elpida F ₅ -3	3911.50 a	105	4.88	24.44 a	102	4.50	162.95 a	104	5.5	
Elpida F ₅ -4	3832.06 a	103	6.55	21.53 a	90	4.81	182.00 a	116	5.7	
Elpida F ₅ -5	2622.13 b	71	3.02	16.50 b	69	3.62	159.83 a	102	4.1	
Elpida F ₅ -6	3114.56 a	84	5.04	18.94 b	79	5.28	166.89 a	106	5.7	
Elpida F ₅ -7	3398.07 a	91	4.20	21.00 a	88	4.52	164.61 a	105	4.9	
Elpida F ₅ -8	3332.67 a	90	3.27	18.67 b	78	6.73	176.66 a	113	4.7	
Iron F ₁	2891.00 b	100	3.19	17.61 b	100	3.64	164.04 a	100	5.0	
Iron HS ₆ -2	2834.06 b	98	3.53	19.39 b	110	4.54	146.87 a	90	5.1	
Iron HS ₆ -3	2665.71 b	92	3.26	17.12 b	97	5.67	154.50 a	94	4.8	
Sahara F ₁	3509.92 a	100	4.67	22.12 a	100	5.12	159.85 a	100	5.6	
Sahara HS ₆ -1	2371.31 b	68	5.41	18.44 b	83	5.10	129.80 a	81	7.4	
Sahara HS ₆ -2	3673.50 a	104	4.04	24.21 a	109	5.61	152.46 a	95	5.5	
Makedonia	2484.44 b		3.32	16.33 b	_	3.66	153.56 a	_	4.7	

Table 4. Total fruit yield (g/plant, fruit number/plant, and g/fruit), vigor/depression (% of its corresponding hybrid), and stability of performance ($\bar{\mathbf{x}}$ /s) of the hybrids and new recombinant inbred lines, in the low-input farming system.

* Entries with the same letter within a column indicate not significant differences, according to Scott-Knott cluster test (a = 0.05).

The recombinant lines of 'Elpida' almost reached the yield of the F_1 hybrid (average lag of 9%). In fact, three provided slightly higher yields in g/plant compared with the hybrid. Lines superior to the F_1 hybrid were characterized by both a high number of fruits as well as a high level of fruit weight (Table 4).

The lines originating from 'Iron' performed almost similar to the F_1 parental hybrid in total yield, and the same was observed for a line originating from 'Sahara', which outperformed the parental hybrid by 4% (Table 4).

All the recombinant lines surpassed the control cultivar 'Macedonia' in total yield. Moreover, the performance of all recombinant lines was more stable in total yield than the early yield (Table 4).

Finally, a high positive correlation between yield per plant and number of fruits per plant was detected (r = 0.97 **), while a low correlation was observed between yield per plant and fruit weight per plant (r = 0.27 **). The results indicated the importance of the characteristic of the number per plant in the breeding process.

3.3. Fruit Quality Traits

The fruit qualitative traits of all tomato cultivars studied are presented in Table 5. In total soluble solids, one recombinant line derived from 'Formula' hybrid (line 1) performed equally to the domestic cultivar 'Makedonia', having excellent quality levels, with 6.50° Brix (Table 5). For total soluble solids, two recombinant lines ('Formula' F₅-7 and 'Iron' HS₆-3) performed equally to or better than the control cultivar 'Makedonia' (Table 5). Specifically, the recombinant lines derived from the 'Formula' hybrid had an average superiority in

total soluble solids content up to 3% over the original hybrid, with the recombinant line 'Formula' F_5 -1 having a significant inbred vigor of 25% (Table 5).

	Fruit Quality Traits								
 Entry	Total Soluble	Solids (°Brix)	Total S	olids (%)					
	x	Vig/Dep	$\overline{\mathbf{x}}$	Vig/Dep					
Formula F ₁	5.20 c *	100	5.68 c	100					
Formula F ₅ -1	6.50 a	125	6.22 b	110					
Formula F ₅ -2	4.77 d	92	5.84 c	103					
Formula F ₅ -3	5.50 c	106	6.17 b	109					
Formula F ₅ -4	4.77 d	92	5.37 d	95					
Formula F ₅ -5	4.87 d	94	5.58 c	98					
Formula F ₅ -6	5.48 c	105	6.45 b	114					
Formula F ₅ -7	5.67 c	109	6.66 a	117					
Formula F ₅ -8	5.38 c	103	6.34 b	112					
Elpida F ₁	5.92 b	100	6.72 a	100					
Elpida F ₅ -1	5.07 d	86	5.83 c	87					
Elpida F ₅ -2	4.97 d	84	5.95 c	89					
Elpida F ₅ -3	4.42 e	75	5.34 d	79					
Elpida F ₅ -4	4.64 d	78	5.84 c	87					
Elpida F ₅ -5	5.27 c	89	5.95 c	89					
Elpida F ₅ -6	5.40 c	91	5.98 c	89					
Elpida F ₅ -7	5.24 c	89	5.94 c	88					
Elpida F ₅ -8	5.38 c	91	5.99 c	89					
Iron F ₁	5.63 c	100	6.21 b	100					
Iron HS_6-2	5.47 c	97	6.05 c	97					
Iron HS ₆ -3	5.77 c	102	6.56 a	106					
Sahara F ₁	4.35 e	100	5.89 c	100					
Sahara HS ₆ -1	3.90 e	90	4.58 d	78					
Sahara HS ₆ -2	4.45 e	102	6.04 c	103					
Makedonia	6.37 a	_	6.96 a	_					

Table 5. Fruit quality traits: total soluble solids (°Brix), total solids (%), and vigor or depression (% of its corresponding hybrid) of F_1 hybrids and their recombinant lines.

* Entries with the same letter within a column indicate not significant differences, according to Scott–Knott cluster test (a = 0.05).

Inbreeding depression was also apparent in some recombinant lines. The germplasm produced from 'Elpida' hybrid had a 15% average inbreeding depression, ranging from 9 to 25%. In the offspring of 'Iron' and 'Sahara' hybrids, the recombinant lines did not differ from the corresponding F_1 hybrid, although a small inbreeding depression of 3% and 10% in 'Iron' HS₆-2 and 'Sahara' HS₆-1 recombinant lines, respectively, was observed. Similar results were obtained for the recombinant lines 'Iron' HS₆-3 and 'Sahara' HS₆-2 (2% inbred vigor, Table 5).

Most of the recombinant lines derived from 'Formula' hybrid provided inbred vigor that reached 17% for total solids content. In contrast, in the recombinant lines derived from the 'Elpida' hybrid, they did not have the original hybrid's total solid content. Among the offspring of 'Iron', the recombinant line 'Iron HS₆-3' exhibited a 6% increase. In contrast to the genetic material originating from 'Sahara', only the recombinant line 'Sahara' HS₆-2 exceeded its original F₁ hybrid, but this was not significant (Table 5).

3.4. Comparing the Two Farming Systems

Comparing the behavior of all genetic material (F_1 hybrids, recombinant lines, traditional cultivar) tested in the two farming systems (Figure 1), a greater dispersion in the total yield values was observed in the high-input system. In contrast, the genetic material evaluated in the low-input system did not exhibit differences. It revealed a smaller range in total yield values when the best entry was used as reference (Figures 2 and 3). The best entry was the recombinant line 'Elpida' F_5 -3 characterized by stability and the highest yield in both farming systems. This may indicate that, to maximize the differentiation between the genetic materials for their description and classification, the breeder should include a high-input system to evaluate during the breeding process.

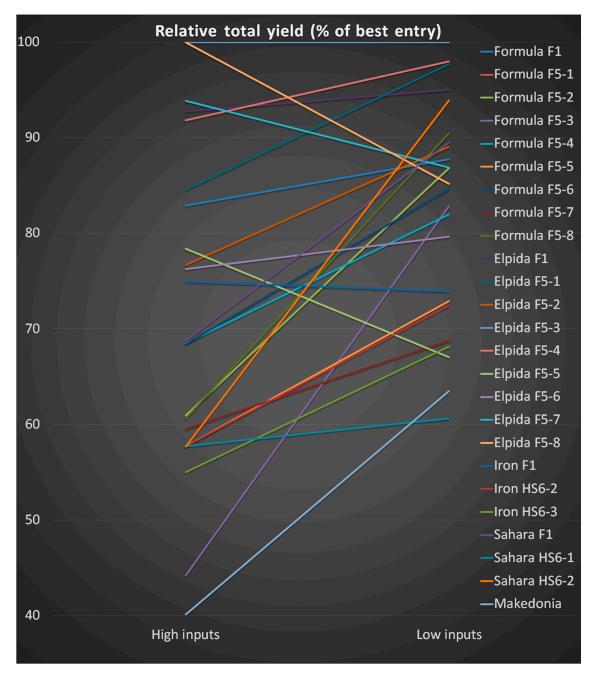


Figure 2. Relative total yield (as % of the best entry) of F₁ hybrids and recombinant inbred lines in two different (high- and low-input) farming systems.

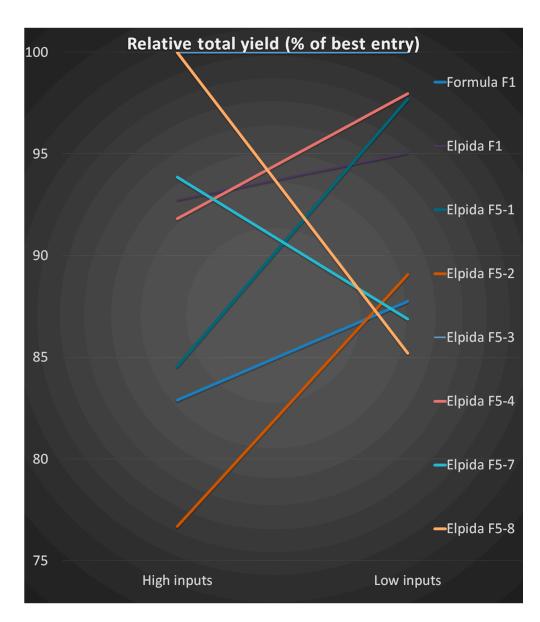


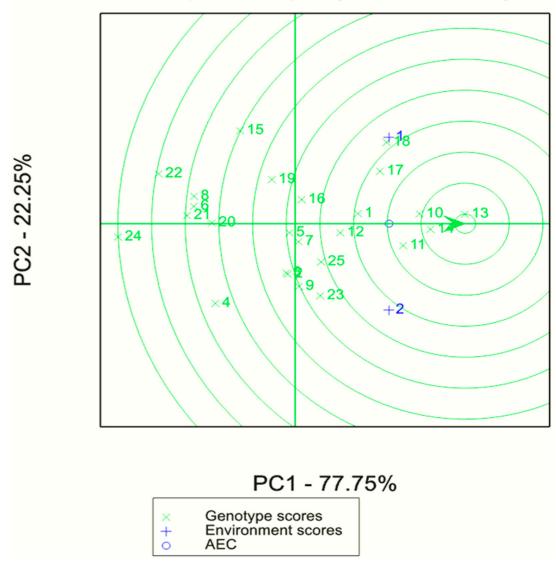
Figure 3. Relative total yield (as % of the best entry) of F_1 hybrids and recombinant inbred lines with high and stable performance in two different (high- and low- input) farming systems.

According to the results, it is important to determine at early stages which is the most suitable genetic material for each cropping system. This approach could cover the future needs of an intensive high-input or low-input organic farming system, which follows sustainability requirements. For example, the recombinant line 'Formula' F₅-3, although it did not perform well in the high-input system (44% of the best genetic material's total yield), performed very well in the low-input system (83% of the best genetic material's total yield) (Table 6). Another example is the recombinant line 'Sahara' HS₆-2. Based on Figure 2, it would not be recommended for a high-input system because it performed only 58% of the best genetic material's total yield. In contrast, this line changes completely when grown in an organic farming system, as it was one of the five best genetic material in total yield, providing 94% of the best entry's ('Elpida' F₅-3) total yield.

Some genotypes were characterized by a high level of homeostasis, and consistently performed well regardless of the cropping system. For example, the recombinant line 'Elpida' F_5 -3 was found to be the best genetic material in either cropping system. This is the reason that, in Figures 2 and 3, the total yield of all genetic material, in both farming systems, was estimated in comparison with 'Elpida' F_5 -3's total yield. Additionally, the

recombinant lines 'Elpida' F₅-8, 'Elpida' F₅-7, 'Elpida' F₅-4, 'Elpida' F₅-1, and 'Elpida' F₅-2 did not fall below the level of 77% in either farming system compared with the best genetic material (Figure 3).

The combined determination of mean performance and stability across the two environments is presented by the genotype and genotype \times environment (GGE) biplot analysis [26,27] (Figure 4). The GGE biplot analysis measures the distance of each cultivar from the 'ideal genotype', and revealed that the genotype with the best mean performance and stability was the recombinant line 'Elpida' F₅-3 (code 13), followed by 'Elpida' F₅-4 (code 14), 'Elpida' (F₁) (code 10), 'Elpida' F₅-1 (code 11), 'Elpida' F₅-7 (code 17), 'Elpida' F₅-8 (code 18), 'Formula' F₁ (code 1), and 'Elpida' F₅-2 (code 2).



Comparison biplot (Total - 100.00%)

Figure 4. Genotype and genotype × environment (GGE) biplot analysis for total yield of the 23 tomato genotypes evaluated: green numbers correspond to genotypes (1 'Formula' F_1 , 2–9 recombinant lines of 'Formula' F_1 , 10 'Elpida' F_1 , 11–18 recombinant lines of 'Elpida' F_1 , 19 'Iron' F_1 , 20–21 recombinant lines of 'Iron' F_1 , 22 'Sahara' F_1 , 23–24 recombinant lines of 'Sahara' F_1 , and 25 'Makedonia'; and blue numbers refer to environments (one = high inputs and two = low inputs). AEC = Average Environment Coordination, PC = Principal Component.

Evaluation	High Inputs	Low Inputs	Sum	Ranking	High Inputs	Low Inputs	Sum
1. Formula F ₁	83	88	171	13. Elpida F ₅ -3	100	100	200
2. Formula F ₅ -1	61	87	148	14. Elpida F ₅ -4	92	98	190
3. Formula F ₅ -2	61	87	148	10. Elpida F ₁	93	95	188
4. Formula F ₅ -3	44	83	127	18. Elpida F ₅ -8	100	85	185
5. Formula F ₅ -4	69	82	151	11. Elpida F ₅ -1	85	98	182
6. Formula F ₅ -5	58	73	131	17. Elpida F ₅ -7	94	87	181
7. Formula F ₅ -6	68	85	153	1. Formula F ₁	83	88	171
8. Formula F ₅ -7	60	69	128	12. Elpida F ₅ -2	77	89	166
9. Formula F ₅ -8	61	90	151	22. Sahara F ₁	69	90	158
10. Elpida F ₁	93	95	188	16. Elpida F ₅ -6	76	80	156
11. Elpida F ₅ -1	85	98	182	7. Formula F ₅ -6	68	85	153
12. Elpida F ₅ -2	77	89	166	24. Sahara HS ₆ -2	58	94	152
13. Elpida F ₅ -3	100	100	200	9. Formula F ₅ -8	61	90	151
14. Elpida F ₅ -4	92	98	190	5. Formula F ₅ -4	69	82	151
15. Elpida F ₅ -5	78	67	145	19. Iron F ₁	75	74	149
16. Elpida F ₅ -6	76	80	156	3. Formula F ₅ -2	61	87	148
17. Elpida F ₅ -7	94	87	181	2. Formula F ₅ -1	61	87	148
18. Elpida F ₅ -8	100	85	185	15. Elpida F ₅ -5	78	67	145
19. Iron F ₁	75	74	149	6. Formula F ₅ -5	58	73	131
20. Iron HS ₆ -2	58	72	130	20. Iron HS ₆ -2	58	72	130
21. Iron HS ₆ -3	55	68	123	8. Formula F ₅ -7	60	69	128
22. Sahara F ₁	69	90	158	4. Formula F ₅ -3	44	83	127
23. Sahara HS ₆ -1	58	61	118	21. Iron HS ₆ -3	55	68	123
24. Sahara HS ₆ -2	58	94	152	23. Sahara HS ₆ -1	58	61	118
25. Makedonia	40	64	104	25. Makedonia	40	64	104

Table 6. Relative total yield (% of the best entry) of the hybrids and inbred lines derived from them in two (high- and low-input) farming systems.

4. Discussion

4.1. Inbred Vigor

The exploitation of heterosis is proving to be an efficient approach for the improvement of tomato. Because of their high yielding potential, tomato hybrids have gained popularity among growers [28]. Tomato hybrids are extensively used in commercial production because growers prefer to grow hybrid-cultivars to maximize their revenues as they are characterized by higher productivity, earliness, and fruit quality [29–31]. However, it is unclear whether hybrids could be appropriate when the target cropping environment is a low-input farming system. Perhaps, the answer to this question could be the simultaneous entry of dynamic pure-line cultivars into a seed market that will target low-input organic systems, or in high-input systems, or simultaneously in both farming systems. This could be accomplished by exploiting the phenomenon of inbred vigor.

Our study indicated that some of the newly selected recombinant tomato lines had inbred vigor and surpassed their corresponding hybrid vigor. Thus, in a high-input system, the inbred vigor of recombinant lines for early yield, fruit number per plant, and fruit weight improved up to 20%, 61%, and 10%, respectively. The inbred vigor of recombinant lines for total yield, fruit number per plant, and fruit weight was increased up to 8%, 19%, and 1%, respectively. As for earliness, there were recombinant lines in a low-input system, characterized by inbred vigor increases up to 25%, 27%, and 27% for yield, fruit number per plant, and fruit weight, respectively. In total yield, the inbred vigor improved up to 5%, 20%, and 16% for yield, fruit number per plant, and fruit weight, respectively. For fruit quality traits, the inbred vigor for total soluble solids of the recombinant lines reached 25%, and 17% for total solids of hybrids.

Observations on tomato breeding provided the type of inheritance of the main traits. Both earliness and total yield ability were referred with dominant, additive, and heterotic type of inheritance [32–34]. Accumulation of dominant and partial dominant genes allows the formation of elite inbred lines equivalent to the high-yielding hybrids, and in some cases, the inbred vigor was greater than hybrid vigor. Smith [35] referred to inbred vigor as transgressive vigor and stated that using inbreeding and selection could develop improved tobacco (Nicotiana tabacum L.) lines, which exceeded the best parent and the F_1 in most of the traits. This was further reinforced by Powers [36], who obtained inbred lines in tomato and barley that retained the advantages attributed to heterosis. Elimination of deleterious genes and the accumulation of favorable alleles via inbreeding and selection were found to improve forage yield by 24% even in an alfalfa population [37]. Analogous results were obtained in tomato by Williams [38], Cuartero et al. [39], and Christakis and Fasoulas [40,41]. Ipsilandis and Koutsika-Sotiriou [42] reported that low inbreeding depression and additive gene action in segregating genetic materials might lead to elite second-cycle inbred lines and, consequently, to high yielding crosses. Additive gene action is of great importance, ensuring heritable and stable performance [16,42,43]. Additive effects are heritable, and as depicted here, are of greater importance than non-additive effects [42]. Therefore, the choice of using hybrids instead of inbred lines as the end-products of a breeding program targeted for growers' cultivation needs must also rest on other non-genetic considerations.

4.2. Methodology

In the present paper, our results indicate that the effectiveness of selection may be improved through the use of a suitable breeding methodology. Self-pollinated species, like tomato, are naturally inbred and tend to be homozygous. Breeding strategies in these species are geared toward producing cultivars that are homozygous. The use of the pedigree selection method, at low plant density under honeycomb design scheme at the first segregating generations of a selfed hybrid, could give better results than mass and recurrent selection [7]. This can give rise to the inbred vigor phenomenon and the production of elite inbred lines. Genter and Alexander [44] stated that, if yield performance of S₁ lines depends mainly on additive effects, the yield of their offspring would be proportional to their yielding performance per se. Thus, selection practiced for improving line performance per se may lead to the accumulation of favorable additive genes. Thus, the methodology that is followed to make these inbred lines is essential for the breeder's success.

The holistic approach to selection in a breeding program, which concerns the simultaneous selection of high-yielding plants, can lead to high-yielding cultivars with outstanding fruit characteristics. The new recombinant lines produced from hybrids showed excellent quality attributes. In some of the recombinant lines, inbred vigor was improved by 17% and 25% compared with their respective hybrid for total solid content and soluble solid content, respectively. Thus, it seems that, for these characteristics concerning the quality of the fruit, the additive gene action predominates, so it is feasible to make inbred vigor more important than hybrid vigor.

4.3. Farming System

The breeding process used to produce these recombinant lines was done under an organic low-input farming system. Afterwards, these new lines were evaluated under both low-input and high-input farming systems. Almost all hybrids gave a number of recombinant lines that produced greater yields than their respective hybrid. This indicated that, when breeding and selection are applied under low-input conditions, it is feasible to produce inbred cultivars characterized by high yield and quality that sometimes have better performance than their original F_1 hybrids. These inbred recombinant lines under high inputs revealed that the cultivars that outyielded their respective hybrids did not have the same performance as in the low system of evaluation. It is possible that the breeding process and selection under low-input farming systems could produce cultivars suitable for high-input agriculture systems. Ceccarelli [45] reported that entries selected under well-managed conditions performed better than local cultivars only under improved management conditions, but not under extreme low-input conditions. Thus, one could

assume that genotypes performing well under high inputs change their performance under low inputs, and vice versa. However, in this case, the low-input breeding process showed that lines selected under low-input breeding maintain high yield performance under lowinput conditions, and in some cases, under high-input conditions. Some of the inbred lines had high homeostasis and were characterized by high yields in both farming systems. This means that there is evidence for the possibility of incorporating individual buffering (homeostasis) from hybrids into inbred line cultivars. These results are in agreement with Janick [46], who found that stable hybrids like 'Elpida', which has been the major hybrid for cultivation in Greece for many years, could give rise to stable inbreds (like 'Elpida' F₅-3). Previous research indicated that cultivars that perform well in conventional systems are not necessarily the best when grown under organic conditions [47,48]. For organic agriculture to continue growing as a viable sector of the food system, new cultivars must be bred with adaptation to the specific soils, nutrient inputs, management practices, and pest pressures found in organic farming systems [49]. Modern agriculture is principally focused on cultivars bred for high performance under high-input systems (fertilizers, water, oil, pesticides), which generally do not perform well under low-input systems. These cultivars are high yielders, but they have negative consequences as they are likely to threaten sustainability. A new paradigm is required, assuring food supply as per demand new cultivars are required to bolster sustainable agriculture. This can be achieved by breeding under organic conditions or low-input production systems [6].

Our results indicated less early and total yield variation among tomato genetic materials under low-input conditions compared with high-input farming systems. However, in comparison, high variation among entries for yield productivity was observed for the high-input farming system. This indicates that, regardless of the breeding methodology a breeder follows to create a new cultivar, the final evaluation process should be included simultaneously in a low-input farming system (which is the environment of selection) as well as a high-input farming system, for better discrimination of the genetic material. In recent years, organic farmers have increased their usage of organic seeds on their farms. They are planting 69% of their acreage with organic seed, which is an increase from 58% in 2009 [50]. The widespread availability of commercial organic seed and certifier requests that growers source more organic seed have contributed to this increase. Most organic growers want organic seed, which requires organic plant breeding [50]. The organic seed that has also been bred for improved performance under organic conditions can serve as an essential tool to help farmers produce successful crops. A range of breeding goals desired for the organic sector, such as yield, resistance to biotic and abiotic stress, and sensory qualities demanded by consumers, do not differ from conventional breeding goals. Still, such traits must be expressed under low-input conditions, which cannot be guaranteed if the selection is made in high-input agronomic backgrounds [4].

5. Conclusions

Tomato lines with inbred vigor that can achieve or even exceed hybrid vigor in productivity and fruit quality characteristics could be developed using the appropriate breeding methodology under low-input (organic) conditions. The honeycomb design applied simultaneously with pedigree selection at the first segregating generations was proven to be a powerful tool for a breeder to improve selection effectiveness and ultimately produce elite inbred recombinant lines. Moreover, breeding and selection under low-input conditions could produce tomato cultivars appropriate for organic low-input agriculture. However, the high-input farming system as an evaluation environment is necessary for the best differentiation and discrimination of this kind of cultivar. As done in this study, final evaluations of promising new cultivars should always be performed under both low- and high-input farming systems to classify them according to the target environment. Author Contributions: Conceptualization, I.D.A.; data curation, I.D.A., R.T., I.M., I.N.X. and A.G.M.; formal analysis, I.D.A. and I.M.; investigation, I.D.A., R.T., I.M., I.N.X. and A.G.M.; methodology, I.D.A., R.T. and A.G.M.; resources, I.D.A., R.T., I.M., I.N.X. and A.G.M.; supervision, I.D.A.; validation, I.D.A.; visualization, I.D.A.; writing—original draft, I.D.A., R.T., I.M., I.N.X. and A.G.M.; writing—review and editing, I.D.A., R.T., I.M., I.N.X. and A.G.M. All authors have read and agreed to the published version of the manuscript.

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